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Antero-lateral Abdominal Scent Glands of Braconine Wasps (Hymenoptera: Braconidae)

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Abstract.—Virtually all members of the Braconinae possess one, two or three pairs of sac-like, glandular invaginations of the unscleritized lateral cuticle between the terga and sterna of their 1st and 2nd metasomal (2nd and 3rd abdominal) segments. These antero-lateral abdominal glands (ALAGs) are present in both sexes, are often partially evaginated when the wasps are disturbed (e.g. handled), and are the source of an odoriferous secretion characteristic of the subfamily. The external surfaces of the exposed glands are typically highly corrugated providing a large evaporative surface area. Light and transmission electron microscopy show the thin cuticular intima of the glands to be lined internally by a layer of squamous epithelial cells overlain on the inner most part of the invagination by irregularly shaped secretory cells which are associated with transcuticular ducts. Overlying all these cells are large pigment-containing cells. The function(s) of the ALAG secretions are at present unknown, but they do not serve as a deterrent to vertebrate predators such as some lizards.

Braconid wasps possess a diversity of exocrine glands (Teles da Silva & Palma 1986; Williams *et al.* 1988; Buckingham and Sharkey 1988; Quicke 1990), mostly located toward the posterior of the metasoma. Aside from those associated with the reproductive tract or with mating (Weseloh 1980; Tagawa 1977, 1983; Field and Keller 1994), little as yet is known about the function of these glands (Quicke 1997). Some odoriferous glands in the related family Ichneumonidae (Townes 1939) and in the ant-mimicking, adeliine braconid *Paradelius* De Saeger (Whitfield 1988) may be protective in function, while the Hagen's glands of male opiine braconids may have mixed courtship and protective roles (Buckingham 1964; Buckingham and Sharkey 1988; Williams *et al.* 1988).

Many museum specimens of braconine wasps have puffy membranous protrusions between the tergites and sternites of the 1st to 3rd metasomal segments. These have previously gone unreported, even in the detailed anatomical studies by Alam (1953). Observations on living wasps and dissections of their metasomas have shown that these structures are sac-like scent glands which are partially evaginated when wasps are handled or otherwise disturbed. This particular set of glands appears to be unique to the Braconinae, a large subfamily containing well over 2000 described species, and no equivalent ones in structure and location have been found in any other subfamily of Braconidae. A pair of antero-lateral glands have been described in the pine sawfly, *Diprion similis* (Hartig), but these open via a vertical orifice in the intersegmental membrane between the 2nd and 3rd abdominal terga, and they are only found in females (Mertins and Coppel 1972). These glands are therefore unlikely to be homologous with those found in the Braconinae. In this paper we describe the structure and distri-

bution of these antero-lateral abdominal glands (ALAGs) and report on some observations relating to their possible function.

MATERIALS AND METHODS

Histological and morphological studies were carried out on specimens of *Atanycolus ulmicola* (Viereck) collected in College Station, Texas, *Digonogastra kimballi* Kirkland and *Bracon mellitor* Say, both reared for biological control studies at Texas A&M University, *Habrobracon hebetor* (Say) reared for biological control in Egypt, an unidentified *Bracon* species collected in Budapest, Hungary and an unidentified *Iphiaulax* species collected in North Queenland, Australia. The distribution of ALAGs among other Braconidae and other genera of Braconinae was determined using aqueous KOH treatment and subsequent dissection of dry museum specimens.

Material for light microscopy was embedded in paraffin wax (*Atanycolus*) or resin (*Bracon, Digonogastra* and *Habrobracon*). Wax-embedded material was fixed in alcoholic Bouin's solution, dehydrated through alcohols, double embedded in celloidin/paraffin wax and sectioned at 5 μm. Sections were stained with haematoxylin/eosin. Resin embedded material was fixed in glutaraldehyde followed by osmium tetroxide, embedded in Spurr's resin and sectioned at 0.5 μm. Sections were stained with 1% Toluidine blue in 1% aqueous sodium borate.

Material for transmission electron microscopy was dissected in insect saline (Ephrussi and Beadle 1939) and fixed for 6 hours in 2% glutaraldehyde, 2% paraformaldehyde, 2% acrolein and 1.5% dimethyl sulphoxide in 0.133 M sodium cacodylate (pH 7.4). After washing, material was post fixed in 2% osmium tetroxide (Hayat 1989). Following fixation the material was embedded in Araldite 502-EMBED 812 Embedding Medium (Mollenhauer 1964). Material was sectioned with a diamond knife using an ultramicrotome from LKB (Ultrotome type 4801 A). 50–70 nm thin sections were post-stained with alcoholic uranyl acetate solution for 30 minutes followed by Reynolds' lead citrate (Reynolds 1963) for 10 minutes. Sections were examined and photographed using a Zeiss 10C transmission microscope at 60 kV on Kodak Electron Microscope Film 4489 (ESTAR Thick Base).

The internal morphology of the ALAG was determined both by the dissection of fresh wasps in 70% ethanol or physiological saline, and by dissecting wasps fixed in alcoholic Bouin's solution. The latter material was dehydrated after dissection, critical point dried, sputter coated with gold and examined using a Cambridge scanning electron microscope (SEM).

The external sculpturing of the ALAG was examined by SEM. Specimens of *Atanycolus, Bracon,* and *Digonogastra* were killed by placing them into alcoholic Bouin's fixative or Carnoy Fluid. Metasomas were removed, dehydrated and critical point dried. Some individuals treated this way died with their ALAGs everted. The specimen of *Myosoma nyanzaensis* Quicke & Wharton illustrated is a museum specimen which had died in culture.

Preliminary tests were run to determine whether gland products function as a predator deterrent. Both spiders (Salticidae) and lizards (Iguanidae) were used as potential predators. Predators were placed in cages with male and female *D. kimballi* and with individuals of the doryctine braconid, *Allorhogas pyralophagus* Marsh, which are similarly sized and coloured to *D. kimballi* but lack ALAGs. Interactions between predators and prey were recorded.

RESULTS

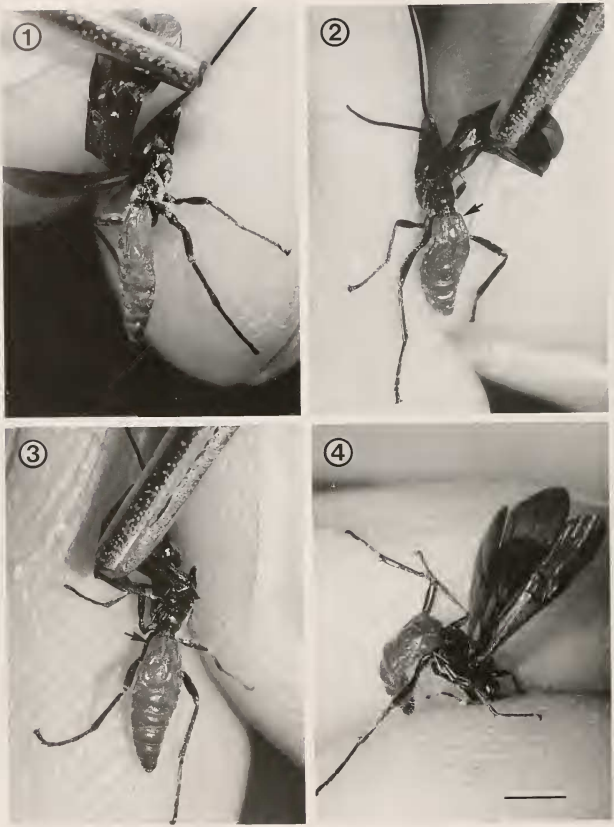
Distribution among genera.—ALAGs were only found in members of the Braconinae and not in any specimens of the related subfamilies Doryctinae, Pambolinae, Rhyssalinae, Exothecinae, Hormiinae,

Rogadinae, Mesostoinae, Histeromerinae, Gnamptodontinae, Opiinae or Alysiinae that were examined (list of taxa sampled available from senior author upon request). Within the Braconinae, ALAG's were present in the vast majority of genera examined, viz. *Angustibracon* Quicke, *Aphrastobracon* Ashmead, *Archibracon* Saussure, *Atanycolus* Foerster, *Bacuma* Cameron, *Baryproctus* Ashmead, *Bathyaulax* Szépligeti, *Bicarinibracon* Quicke & Walker, *Bracon* Fabricius, *Calcaribracon* Quicke, *Callibracon* Ashmead, *Campyloneurus* Szépligeti, *Compsobracon* Ashmead, *Compsobraconoides* Quicke, *Cratobracon* Cameron, *Cratocnema* Szépligeti, *Cyclaulax* Cameron, *Cyclaulacidia* Quicke, *Digonogastra* Viereck, *Eunesaulax* Tobias, *Euurobracon* Ashmead, *Euurobraconoides* Quicke, *Euvipio* Szépligeti, *Fraterarchibracon* Quicke, *Gammabracon* Quicke, *Glyptomorpha* Holmgren, *Gronaulax*, Cameron, *Habrobracon* Ashmead, *Hemibracon* Szépligeti, *Hybogaster* Szépligeti, *Iphiaulax* Foerster, *Ischnobracon* Baltazar, *Lapicida* Quicke, *Lasiophorus* Haliday, *Leptobracon* Szépligeti, *Ligulibracon* Quicke, *Macrobracon* Szépligeti, *Megalommum* Szépligeti, *Merinotus* Szépligeti, *Mesobracon* Szépligeti, *Mollibracon* Quicke, *Monilobracon* Quicke, *Myosoma* Brullé, *Nedinoschiza* Cameron, *Nesaulax* Roman, *Odesia* Cameron, *Odontoscapus* Kriechbaumer, *Paranesaulax* Quicke, *Philomacroploea* Cameron, *Plaxopsis* Szépligeti, *Pseudovipio* Szépligeti, *Psittacibracon* Quicke, *Pycnobracon* Cameron, *Rhadinobracon* Szépligeti, *Rhytimorpha* Szépligeti, *Rostraulax* Quicke, *Serraulax* Quicke, *Shelfordia* Cameron, *Sobrinarchibracon* Quicke, *Sororarchibracon* Quicke, *Stenobracon* Szépligeti, *Stigmatobracon* Turner, *Sylvibracon* Quicke, *Undabracon* Quicke, *Vipiellus* Roman, *Vipio* Latreille, *Vipiomorpha* Tobias, *Virgulibracon* Quicke, *Virgulibraconoides* Quicke, *Vomeribracon* Quicke, *Zaglyptogastra* Ashmead and *Zanzopsis* van Achterberg.

The only Braconinae examined in which ALAGs appeared to be absent are *Mesobraconoides psolopterus* (Wilkinson) and a *Pseudoshirakia* species, both belonging to the *Mesobracon* Szépligeti group of genera (Quicke 1987; Sarhan and Quicke 1990), and a *Rhamnura* species of the Rhamnurini.

In most genera there were two or three pairs of ALAG sacks but in a few, for example in *Lasiophorus*, *Leptobracon* and *Sobrinarchibracon*, only one was apparent. The ALAG in *Coeloides* is poorly developed and is also more or less unilobular. Details of gland number and sculpture may prove useful in future phylogenetic analysis of the relationships between the genera of Braconinae.

Behaviour.—As with many Apocrita, including both aculeates and terebrants, male and female braconines often raise their metasomas vertically and flex them when handled. In the case of females of some braconines, particularly those with a moderately short, robust ovipositor (e.g. some *Iphiaulax* Foerster and *Digonogastra* Viereck), this may result in stinging (Quicke *et al.* 1992). For many species (and all males) pseudo-stinging behavior is mimetic (see Rothschild 1984; Quicke 1986a, b). In both male and female Braconinae, this abdominal flexion is also frequently accompanied by various degrees of eversion of the ALAG (Figs. 1–4) and the latter is associated with the release of a distinctive odour. However, eversion of the glands does not always accompany metasomal flexion and flexion itself is probably principally concerned with applying the metasomal apex to the source of disturbance as part of the stinging or pseudo-stinging behaviour. In living *D. kimballi*, small droplets of a clear fluid can be observed on the everted ALAG and this liquid can be collected by touching the end of a fine glass capillary to the droplets. The liquid appears to contain both highly volatile and less volatile components since the droplet rapidly volatilizes in air, but leaves a sticky residue. Some alcohol-preserved specimens of this and many other



Figs. 1–4. Photographs of live male *Digonogastra kimballi* being handled so as to evoke eversion of the antero-lateral abdominal glands (arrows in Figs. 2–4), and pseudo-stinging posture (Fig. 4). Scale bar approximately 2 mm.

species of Braconinae have their ALAGs filled with a pale grey precipitate similar to that observed by Buckingham in the intersegmental, tergal glands of similarly preserved *Bracon* species (Buckingham 1964).

Palatability of braconines.—Despite their distinctive odour and the aposematic coloration of many of the larger species (Quicke 1986a; Quicke *et al.* 1992), at least *Atanycolus simplex* and *Digonogastra kimballi* appear to be palatable to several potential predators. One of us (DLJQ) has eaten *A. simplex,* which have a weak but not unpleasant flavour. Lizards (*Sceloporus cyanogens*) presented with male and female *D. kimballi* consume them readily, but spiders (*Platycryptus undata* (DeGeer)) release the wasps rapidly after an attack. A wasp and spider will both remain alive for a week if placed together in a small vial even if the spider has no alternative food source. However, the doryctine *A. pyralophagus* elicited a similar response, and other observations have shown that several non-braconine Braconidae are also unpalatable to spiders (Wharton 1984).

Morphology and histology of glands.—Dissections and SEM of the external surface of the ALAG revealed that there are one, two or three discrete pairs of evaginations (Figs. 5–12). In freshly dissected material of *D. kimballi* or *A. ulmicola,* the inner surface of these evaginations is covered by large red-pigment-containing cells and there are no obvious muscular attachments to the ALAG membrane (Figs 11, 12).

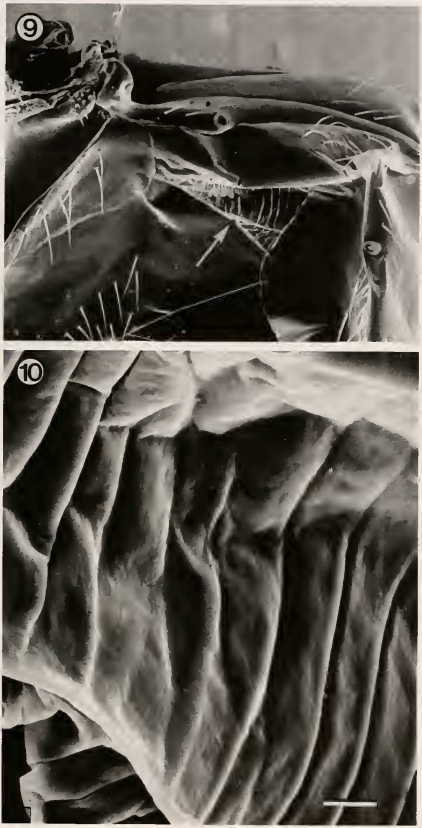
Externally, the surface of the ALAG in each of the five genera examined (*Atanycolus, Bracon, Digonogastra, Habrobracon* and *Myosoma*) was highly corrugated although there were marked differences in the detailed form of the surface sculpture between them (Figs. 5–10). No pores were apparent on evaginated sacs under the SEM, however, cuticular ducts were usually discernible in chlorazol black-stained, KOH-treated sac cuticle. Ductules were also observed in some semi-thin sections when these were examined carefully at 200 × magnification (Fig. 15). In most genera of Braconinae, these ducts were located on the innermost portion of the sac. In semi-thin sections they were specifically associated with a patch of irregularly-shaped subepidermal cells whose cytoplasm stained darkly with toluidine blue (Fig. 16; S).

Transverse light microscope sections through ALAGs showed a deeply invaginated chitinous membrane (intima). The chitin lining the sac was thinner and less densely staining with toluidine blue than that of the adjacent entrance slit to the sac which was in turn thinner than the adjacent cuticle that was never invaginated into the gland sac (Fig. 14). Light microscope sections also revealed ducts running from the cell layer lining the ALAG membrane and the external surface of the gland (Fig. 15 arrow). These secretory ductules appear to pass directly from epithelial to secretory cells and therefore the latter can be classified as Type 3 gland cells as defined by Noirot and Quennedey (1974) and Quennedey (1975).

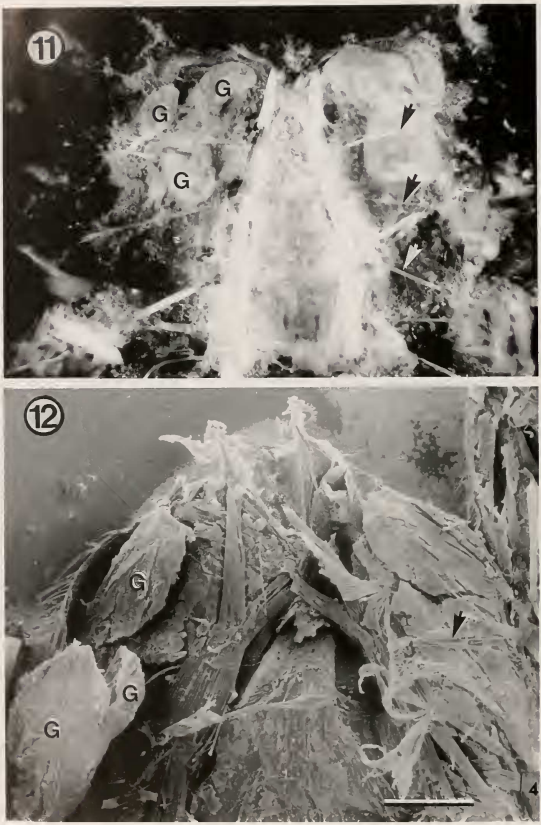
The secretory gland cells themselves are characterized by the possession of a complex, elongate, microvilli-lined secretory invagination or end apparatus (Figs. 17–20). Running along the center of the invagination is a cuticular structure which in cross-section shows a thin and frequently interrupted circumferential layer within which is a thicker zone of longitudinally-orientated, cuticular filaments. Usually a discrete lumen can be discerned surrounded by microvilli (Fig. 19).

The secretory gland cell cytoplasm contains numerous elongate to irregular mitochondria and is densely packed with small, (0.04–0.08 μm), irregular, membrane-bounded vesicles (Figs. 18, 19). There are free ribosomes and dilated rough endoplasmic reticulum (indicating an active phase) within the cytoplasm. Microtubules can be detected more frequent-

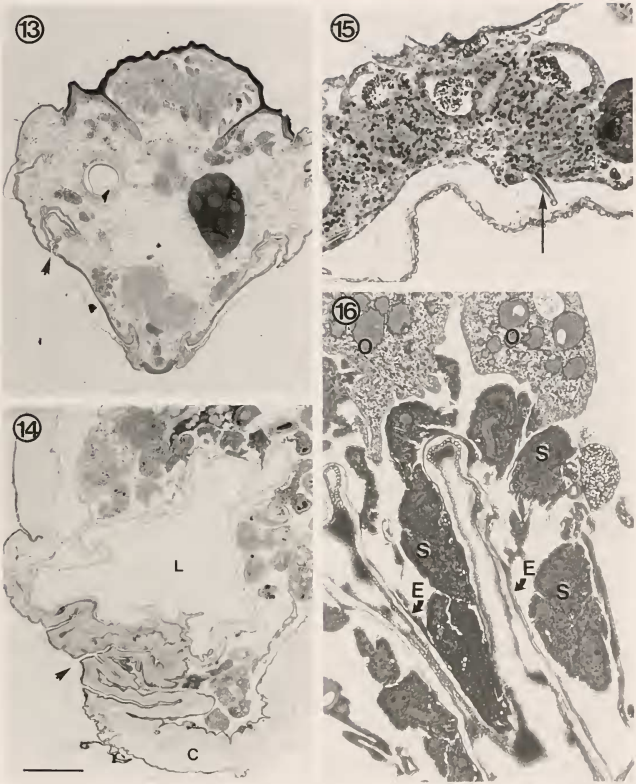
Figs. 5–8. SEMs of external appearance of ALAGs: 5, 6, right anterior metasoma, *Digonogastra kimballi* showing, everted (5) and uneverted, resting (6) condition. 7, 8, left anterior metasoma, *Bracon mellitor* showing everted ALAGs. Scale bar on Fig 8 applies to all figures on plate. Scale bar applied to: 5, 6 = 0.25 mm; 7 = 0.1 mm; 8 = 0.05 mm.



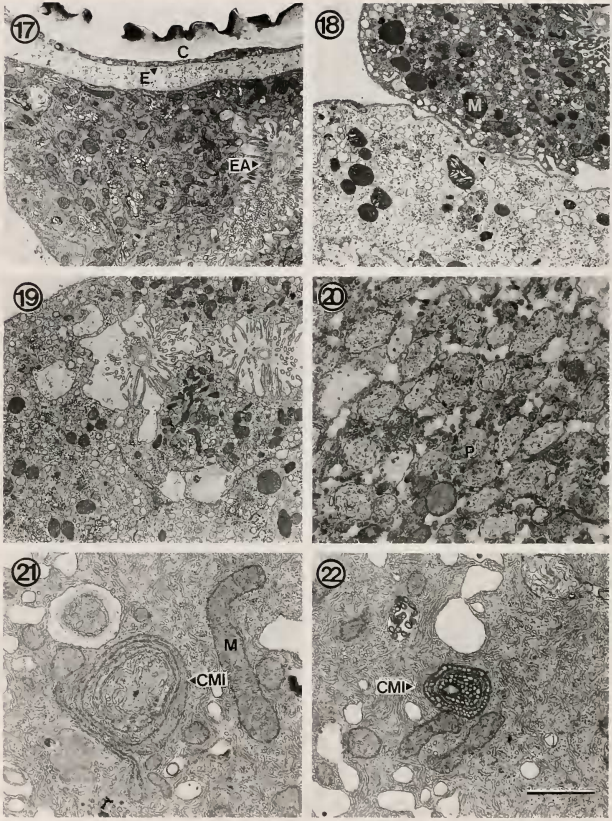
Figs. 9–10. SEMs of external appearance of partially everted ALAG of *Myosoma nyanzaensis* showing surface sculpture at two magnifications. Scale bar on Fig. 10 applies to both figures on plate. Scale bar applied to: 9 = 0.1 mm; 10 = 0.01 mm.



Figs. 11–12. Light and scanning electron micrographs of dissected anterior metasomas (anterior at top) of *Digonogastra kimballi* (9) and *Iphiaulax* sp. (10), showing internal appearance of non-evaginated ALAGs. Abbreviations: G = gland sac; arrows indicate segmental muscle strands overlying gland sacs. Scale bar on Fig. 12 applies to both figures on plate. Scale bar applied to: 11 = 0.5 mm; 12 = 0.25 mm.



Figs. 13–16. Light photomicrographs of semi-thin, resin-embedded, transverse sections of ALAGs in *Bracon* sp. (13, 14) and *Digonogastra kimballi* (15, 16). Abbreviations: C = cuticle; E = epithelial cell; L = lumen of ALAG; O = oenocyte/pigment cell; S = secretory cell; arrows in 13 and 14 indicate opening of ALAG sac to exterior; arrow in 15 shows pore through glandular cuticle. Scale bar on Fig. 14 applies to all figures on plate. Scale bar applied to: 13 = 0.1 mm; 14, 15 = 0.05 mm; 16 = 0.025 mm.



Figs. 17–22. Transmission electron micrographs showing ultra-structure of ALAG and related cells in *Digonogastra kimballi*. 17, secretory cell (note microvilli-lined ductule) separated from cuticle with associated epithelial cell; 18, 'dark' secretory cell (upper right and translucent type of secretory cell with numerous large pale inclusions (lower left); 19, secretory cell with looped end apparatus ductule sectioned twice, note the numerous mitochondria; 20, pigment cell; 21 and 22, oenocytes showing extensive smooth endoplasmic reticulum, elongate mitochondria and membranous structures. Abbreviations: C = cuticle; CMI = complex membranous inclusion; E = epithelial cell; EA = end apparatus; M = mitochondrion; P = putative pigment inclusion. Scale bar on Fig. 22 applies to all figures on plate. Scale bar applied to: 17, 19 = 1.0 μm; 18 = 0.5 μm; 20–22 = 2.0 μm.

ly near the base of the microvilli, next to invaginations. Numerous Golgi complexes were discernible, located at some distance from the secretory ductule. Some secretory cells appeared rather less electron lucid than others (Fig. 18; upper right *cf* lower left) but all had a similar complement of subcellular organelles.

The gland cells, and on the more peripheral part of the gland sac, the epithelial cells, are overlain by large pigment-containing lipid cells (Figs. 11, 12, 16). Under the transmission electron microscope these pigment-containing cells were packed with large, weakly-staining, membrane-bounded droplets (Fig. 20; P) which we interpret as being a lipid-based pigment. Between these, the cytoplasm has extensive and relatively dark-staining smooth endoplasmic reticulum. Scattered over and among the pigment cells were a number of another category of large cells which SEM revealed to be oenocytes (Fig. 14). These were densely packed with smooth endoplasmic reticulum interspersed with elongate mitochondria (0.5–2.0 μm long by 0.2–0.4 μm). The oenocyte sections also showed a number of complex membranous inclusions (Figs. 21, 22).

DISCUSSION

The present paper describes a set of unique, eversible, sac-like glands, the ALAGs, that are located laterally at the anterior end of the metasoma in virtually all members of the braconid subfamily Braconinae. These glands are the source of a distinctive odour which is characteristic of members of the Braconinae (Quicke 1988) and they are everted and release their secretory product notably when the wasps are disturbed in some way, such as when they are handled or caught in an insect net. The end apparatus of the gland cells and vesicular organelles are very similar to those of the venom glands and other glands associated with reservoirs suggesting that the anterolateral glands may be very active secretory structures.

Undoubtedly, some parasitic wasps (including ichneumonids and braconids) produce volatile secretions that render them unpalatable to potential predators (Townes 1939; Buckingham & Sharkey 1988; Wharton 1984). The function of the ALAGs in the Braconinae is still obscure, however. Although the product seems to be released when the wasps are disturbed, it does not appear to render the wasps unpalatable to vertebrates. Although braconines are rejected by salticid spiders, members of several other braconid subfamilies that do not have an obvious odour and lack ALAGs are similarly rejected. A sex pheromone function for the ALAGs does not seem likely since the glands are well-developed in both sexes, and, in addition, members of both sexes have a similar odour to humans. However, in a behavioral study on *Habrobracon*, Grosch (1948) showed that males were attracted more by the anterior of the female metasoma than by its posterior part. If the gland in females does serve as a male attractant, then the question still remains as to what the role of the ALAGs might be in male braconines. Perhaps the ALAG product has a more general intra-specific signalling role such as an aggregation or alarm pheromone.

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